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# The basic reproduction quotient ( $Q_0$ ) as a potential spatial predictor of the seasonality of ovine haemonchosis

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**Abstract.** *Haemonchus contortus* is a gastrointestinal nematode parasite of small ruminants, which feeds on blood and causes significant disease and production loss in sheep and goats, especially in warmer parts of the world. The life cycle includes free-living immature stages, which are subject to climatic influences on development, survival and availability, and this species therefore exhibits spatio-temporal heterogeneity in its infection pressure based on the prevailing climate. Models that better explain this heterogeneity could predict future epidemiological changes. The basic reproduction quotient ( $Q_0$ ) was used as a simple process-based model to predict climate-driven changes in the potential transmission of *H. contortus* across widely different geo-climatic zones, and showed good agreement with the observed frequency of this species in the gastrointestinal nematode fauna of sheep ( $r = 0.81$ ,  $P < 0.01$ ). Averaged monthly  $Q_0$  output was further used within a geographical information system (GIS) to produce preliminary haemonchosis risk maps for the United Kingdom (UK) over a four-year historical span and under future climate change scenarios. Prolonged transmission seasons throughout the UK are predicted, especially in the south although with restricted transmission in peak summer due to rainfall limitation. Additional predictive ability might be achieved if information such as host density and distribution, grazing pattern and edaphic conditions were included as risk layers in the GIS-based risk map. However, validation of such risk maps presents a significant challenge, with georeferenced observed data of sufficient spatial and temporal resolution rarely available and difficult to obtain.

**Keywords:** basic reproduction quotient, geographical information system, *Haemonchus contortus*, risk maps, spatial prediction, climate change, epidemiology.

## Introduction

*Haemonchus contortus* is a blood-feeding nematode parasite of the gastrointestinal (GI) tract of small ruminants that - along with other GI nematodes - causes substantial disease and production impact in livestock worldwide (Charlier et al., 2014a), especially in warm climatic regions. Adult worms are parasitic in the abomasum, and females lay eggs that pass out in the faeces, where they develop through first and second larval stages to the infective third larval stage (L3). The L3 moves out of the faeces and onto the herbage, where it is ingested by a future host. Due to the warm and moist conditions required by the free-

living stages for development and translation onto herbage (O'Connor et al., 2006), there is significant potential for spatial and temporal heterogeneity in the infection pressure of *H. contortus* based on prevailing climate and weather conditions. By understanding this heterogeneity, predictions of disease risk can be generated and potential effects of climate change on parasite ecology and epidemiology explored (Morgan and Wall, 2009; Van Dijk et al., 2010; Fox et al., 2012). In particular, successful mapping of *H. contortus* infection pressure could serve as an early warning system (EWS) for stakeholders, particularly farmers and their advisors; thus guiding effective and efficient strategic control plans (Van Wyk and Reynecke, 2011; Kenyon et al., 2009).

In practice, infection with *H. contortus* is likely to be complex and related to an array of management variables as well as climatic factors. Thus, although mathematical models of the population dynamics of *H. contortus* and its dependence on climate have been constructed previously (Smith, 1994), these tend to be

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limited in the extent to which they incorporate important management factors (Morgan, 2013), or alternatively include such factors but lack the transparency needed in order to separately explore effects of climate (Learmount et al., 2006). We take an alternative, simplifying approach. The strong influence of climate on the availability of infective *H. contortus* larvae, and the particularly high biotic potential of this species among the gastrointestinal nematodes of ruminants, is such that a simple index of climatic suitability for successful maturation of the free-living stages could itself be a useful predictor of transmission. The basic reproduction quotient ( $Q_0$ ) was devised as such an index based on the widely used basic reproduction ratio ( $R_0$ ) for micro-parasites (Roberts and Heesterbeek, 1993; Heesterbeek and Roberts, 1994).  $R_0$  represents the number of hosts that are infected from each infected host, with  $R_0 > 1$  signifying the potential for an epidemic to grow.  $Q_0$  for macroparasites is similarly defined as the average number of adult female worms produced by one female worm in the absence of density-dependent constraints during its entire reproductive lifespan when introduced into a previously unexposed host population (Heesterbeek and Roberts, 1995).  $Q_0$  therefore measures the maximum reproductive potential of a parasite between one generation and the next in the absence of any density-dependent constraint (Scott and Smith, 1994). As a threshold quantity,  $Q_0$  is a simple estimate of the long-term trajectory of the parasite population (Anderson and May, 1991; Roberts, 1995). Similarly to  $R_0$ ,  $Q_0$  values less than unity indicate that environmental conditions are not conducive for persistence of the parasite population, should those conditions prevail. On the other hand, a  $Q_0$  value  $\geq 1$  implies a tendency towards population growth in the absence of host immunity with resultant higher infection pressure. In effect, the  $Q_0$  model should be able to identify conditions or factors that will affect the parasite's transmission potential (Grenfell and Dobson, 1995; Kao et al., 2000).

The present study aimed to explore the application of  $Q_0$  as a predictor of spatio-temporal variation in transmission potential. Thus, the objectives were: first, to determine whether predicted  $Q_0$  correlates with the observed occurrence of *H. contortus* infections in sheep across contrasting geo-climatic zones; second, to explore the spatial application of  $Q_0$  in the form of maps at the national level using the United Kingdom (UK) as a case study; third, to dissect the components of  $Q_0$  to identify and understand the role of different climatic variables in the predicted spatio-temporal variation of haemonchosis and, finally, to extend the

model to identify the possible impacts of climate change on disease risk in future. The intention was to identify the potential for further development of  $Q_0$ -based approaches for this climate-sensitive parasite species.

## Materials and methods

### Assumptions of the $Q_0$ model

We aimed at developing a simple, dynamical  $Q_0$  model, universally adaptable to any region, and only relying on climate drivers. The exclusion of management processes allows the present model to focus on how climate changes drive the availability of the free-living stages for host infection in space and time. Specific simplifying assumptions include the fact that the host population is grazed continuously on pasture, where all the free-living stages, particularly the infective  $L3$ , are evenly dispersed (Kao et al., 2000); there is no control regimen or grazing management; only free-living stages are affected by climate (Kao et al., 2000; Kahn, 2010) and the host population is assumed to be immunologically naive.

### Model construction

The  $Q_0$  model is deterministic and is calculated as follows:

$$Q_0 = \underbrace{\frac{\lambda}{2\mu_p}}_{\text{Term 1}} * \underbrace{\frac{d_e d_b}{(\mu_e + d_e)(\mu_{l3} + d_b)}}_{\text{Term 2}} * \underbrace{\frac{cH}{bA\mu_{lb} + cH}}_{\text{Term 3}} * \underbrace{pe}_{\text{Term 4}}$$

where  $\lambda$  represents the fecundity of females (eggs produced per female per day), which is divided by two to take account of the sex ratio;  $\mu_p$  the mortality rate of adults in the host;  $d_e$  development rate from egg to  $L3$ ;  $d_b$  the migration rate of  $L3$  from the faeces onto herbage;  $\mu_e$  the mortality rate of eggs;  $\mu_{l3}$  the mortality rate of  $L3$  in faeces;  $c$  the daily larval ingestion rate per host;  $H$  the host density;  $b$  the standing biomass;  $A$  the grazed area;  $\mu_{lb}$  the temperature-dependent mortality rate of  $L3$  on pasture; and  $pe$  the establishment rate of  $L3$  (Rates are expressed per day, areas as hectares, and biomass and herbage intake in kg).

The breakdown of the model into four terms is useful for understanding the relation of  $Q_0$  to phases of the parasite life cycle, thus:

- (i) Term 1 = lifetime reproductive output.
- (ii) Term 2 = probability of development to  $L3$  and successful migration of  $L3$  onto herbage.

- (iii) Term 3 = probability of ingestion of *L3* by a susceptible host through grazing.
- (iv) Term 4 = probability of establishment of *L3* once ingested and maturation to become a reproducing adult.

The model parameters are either constants, or vary dynamically with the climate (specifically temperature and rainfall). In order to assess the impact of rainfall limitation on the transmission of *H. contortus*, a variant of  $Q_0$  was run based only on temperature, by removing rainfall-related constraints on larval development, survival and translation onto herbage. This nested derivative of  $Q_0$  was represented as  $Q_{0t}$ . Parameter values were estimated by literature review. Further details on the construction of the model and the parameters used are given in the complementary supplement material (CSM).

### Validation

To assess the reliability of  $Q_0$  as a spatial predictor of *H. contortus* transmission across different geo-climatic regions, data on rainfall, temperature and haemonchosis burden were sourced across climatically diverse countries. Climatic variables were rainfall and temperature from the nearest available point (<http://www.worldclim.org>). Data on the haemonchosis burden in field populations of sheep or goats consisted of either *post mortem* recovery of adult worms (PM), recovery of *L3* from pasture (*L3*) or faecal egg counts with larval culture to characterise the specific proportion of *H. contortus* (FEC). These three haemonchosis indices were utilised in this study and taken to represent the proportion of the total counts that were *H. contortus* over all seasons sampled. The data search was designed to cover a broad range of eco-climatic zones based on the Koeppen-Geiger climate classification. Altogether, data were obtained for 25 different locations (see CSM).  $Q_0$  was run to predict the overall average climatic conditions for *H. contortus* transmission at each location by using respective data on temperature and rainfall, at weekly or monthly resolution as available, and then averaged on an annual basis to arrive at mean annual model predictions. Where only monthly rainfall was recorded, it was assumed to be evenly distributed over the four weeks of the month. Mean  $Q_0$  was compared with the proportion of *H. contortus* observed in order to test the ability of the model to distinguish between locations that had a propensity to support dominance of this species from those that did not.

### Mapping $Q_0$ at the sub-national level

UK was used as a case study because of ready availability of climate data, and current concern around possible future impacts of climate change on ovine haemonchosis (Kenyon et al., 2009). A 25-km gridded monthly dataset for the whole of the UK for both temperature and rainfall was provided for the period 2003 - 2006 by the UK Met Office (UKCP09; available on request via the website). Future estimates of temperature and rainfall for the 2020s and 2080s were also obtained from the UKCP09 based on low and high projected emission scenarios (2020Lo, 2020Hi, 2080Lo, 2080Hi) (Murphy et al., 2009).

In order to compare the role of rainfall to that of temperature in generating transmission potential,  $Q_0$  predictions (from both temperature and rainfall) and  $Q_{0t}$  predictions (from temperature alone) were calculated. Each version of  $Q_0$  was then used as the only data-layer to construct a geographic information system (GIS)-based climate-driven haemonchosis risk map, using ArcMap version 10 (ESRI, Redlands, CA, USA) software.

### Results

Output from the  $Q_0$  model was first compared with observed level of *H. contortus* infection in small ruminants in different parts of the world, as broad-ranging point validation of model predictions regarding climatic suitability for development and transmission. Thereafter, the  $Q_0$  model was applied on a spatial grid at the national scale (UK); before being subjected to exploration using future climate change scenarios.

### Reliability test of $Q_0$ as a spatial predictor of *H. contortus*

Predicted annual average  $Q_0$  was significantly correlated with the observed proportion of *H. contortus* in samples of adult worms, and larvae cultured from faeces and recovered from pastures (Pearson  $r_{25} = 0.81$ ,  $P < 0.01$ ; Fig. 1). General differences in the proportion of *H. contortus* reported in different Koeppen-Geiger eco-climatic categories were reflected in predicted  $Q_0$  (Fig. 2); thus, for example, tropical > temperate areas for both variables. Differences between locations with similar eco-climatic characteristics were also consistent with  $Q_0$  in many cases; for example, Cuba > Ethiopia and Albany, Australia > Greece. This provides qualitative support for the ability of the model to predict broad differences in climatic suitability for transmission of *H. contortus*.

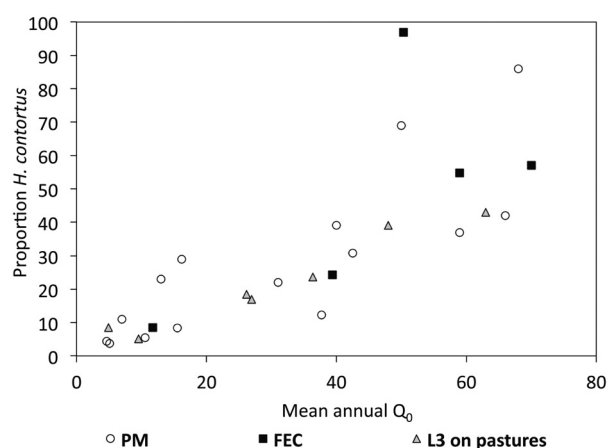


Fig. 1. Mean annual predicted  $Q_0$  for *H. contortus* against the mean proportion of total parasite counts comprising *H. contortus* for 25 geo-climatic locations. Parasite counts were from *post mortem* recovery of adult worms (PM), faecal egg counts cultured to allow specific identification of larvae (FEC), and infective larvae recovered from pasture (L3).

#### $Q_0$ -based UK risk map

For each year from 2003 to 2006,  $Q_0$ -based risk maps for the UK revealed that the summer months (June - September) constituted the highest climatic risk for ovine haemonchosis. This risk was predicted to decrease in autumn, as temperatures decreased, first in the north and then further south (shown in Fig. 3 for 2003, with other years 2004-2006 providing very sim-

ilar patterns). In the whole of UK, the risk of  $L3$  development was predicted to be absent in the winter months (December - February). This general seasonal pattern agrees with that found in laboratory diagnoses of *H. contortus* infection in sheep in the UK (van Dijk et al., 2008), which provides qualitative validation of the model. The risk map for August 2003 indicated that there was reduction in the predicted haemonchosis risk in some parts of central-south and east England. Comparing  $Q_0$ , which included constraints on  $L3$  development and survival under low rainfall conditions, with  $Q_{0t}$ , in which this constraint was absent, identified that moisture limitation accounted for this apparent paradox (Fig. 4). In all other months and years examined, maps of  $Q_0$  and  $Q_{0t}$  did not differ, indicating that moisture was not limiting to transmission in the model.

When projected climate change scenarios were applied to the  $Q_0$  model, spatio-temporal distribution of risk changed substantially. Examples are shown in Fig. 5 for key months with respect to the 2003-2006 period and projected 2080s high emissions scenarios, which were representative of key predicted patterns. Rainfall limitation was predicted to increasingly suppress *H. contortus* transmission in the south of the UK in peak summer, while higher temperatures were predicted to support transmission in more northern regions. In other months, conditions were predicted to be better for transmission, leading to a prolongation of

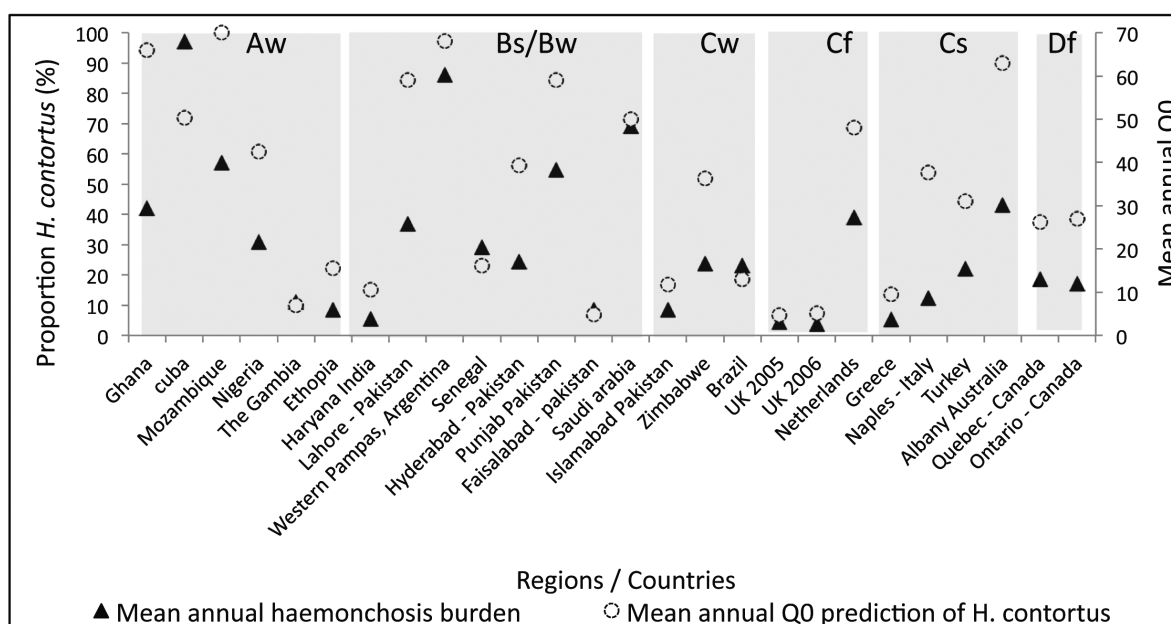


Fig. 2. Mean annual predicted  $Q_0$  for *H. contortus* and the average proportion of total parasite counts comprising *H. contortus* for 25 geo-climatic locations (see Fig. 1 above). Locations are arranged based on the eco-climatic zones of the Koeppen-Geiger classification of climate, thus: Aw = tropical savannah; Bw = hot desert; Bs = hot semi-arid; Cw = subtropical; Cf = oceanic; Cs = Mediterranean; Df = continental.



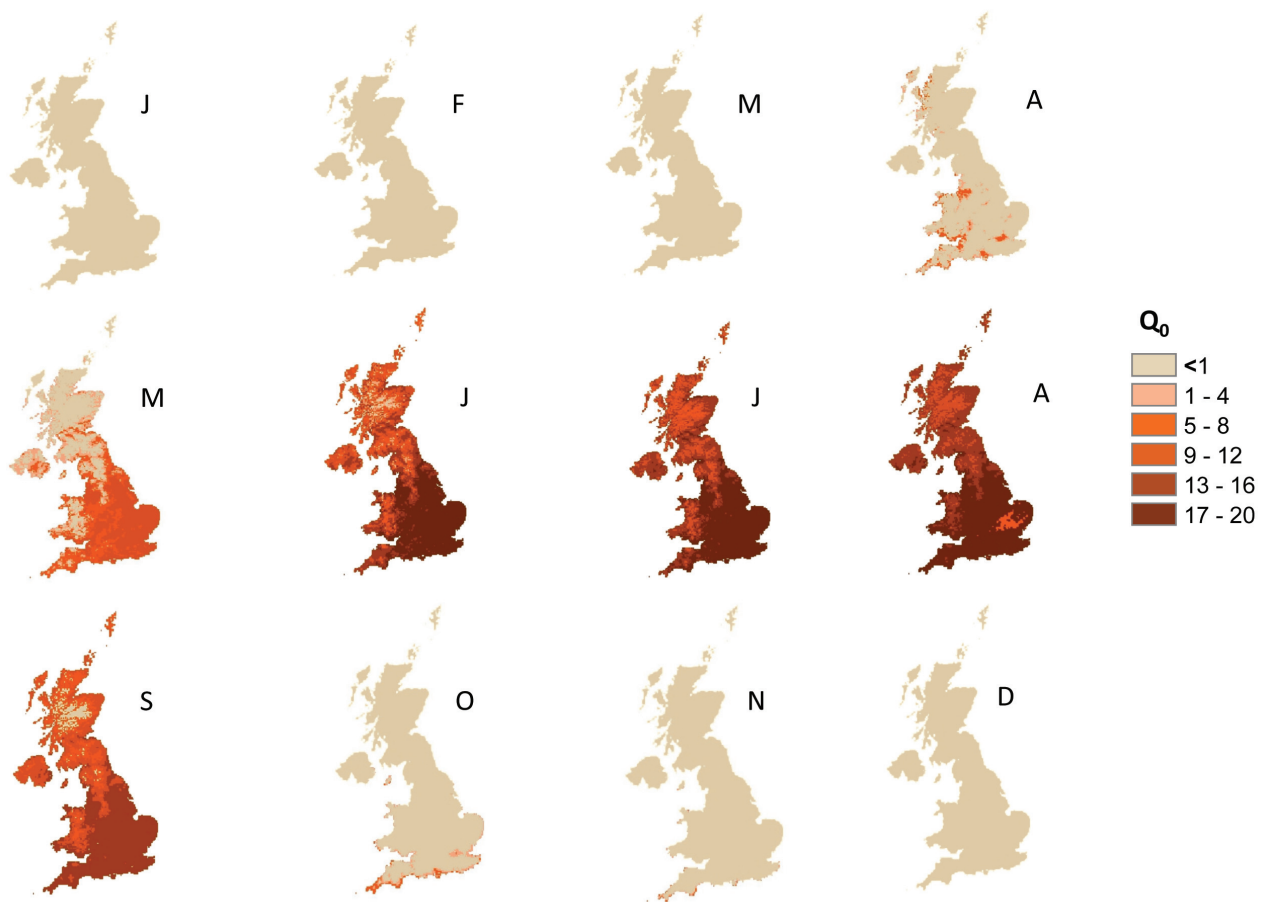


Fig. 3. Monthly GIS-based  $Q_0$  risk map showing the geographic distribution and predicted relative risk of *H. contortus* infection pressure across the UK using climatic data from 2003.

the risk period throughout the country and the possibility of year-round transmission in the South, where  $Q_0$  exceeded unity even in the coldest winter months of December and January. As in the historical time series, the period during which  $Q_0 > 1$  was as much as four months longer in areas of the South than in northern Scotland under climate change scenarios.

## Discussion

Knowledge and understanding of how climate supports or inhibits *H. contortus* transmission can provide a basis for farmers and their advisers to make farm decisions for strategic and sustainable parasite control. These decisions can help to keep *H. contortus* populations at an economically acceptable level in grazing sheep without encouraging selection for anthelmintic resistance through excessive treatment (Van Wyk and Bath, 2002; Van Wyk and Reynecke, 2011; Falzon et al., 2014). Essentially, information on spatio-temporal variation in climatic suitability for the availability of *L3* for infection of sheep, given pasture contamination with *H. contortus* eggs, should allow good farm management decisions to be made for cost-effective and sustainable control. Among parasites of sheep, *H. contortus* is a suitable candidate for such a climate-driven approach, since its ubiquity and high biotic potential mean that egg output is often high, and propagation of infection is largely driven by climate with rapid development of infective larvae under



Fig. 4. Comparison of the roles of rainfall and temperature in predicted *H. contortus* transmission potential across the UK using climatic data from August 2003.  $Q_{0t}$  represents a nested model of  $Q_0$  that is unconstrained by moisture limitations on larval development, translation to pasture and survival.



Fig. 5. Comparison of predicted  $Q_0$  under historic (2003-06 averaged) and projected future climates, using the UKCP09 high emissions scenario.

optimum conditions (O'Connor et al., 2006, 2008). This paper builds on earlier efforts to combine climate-driven aspects of nematode population dynamics into a simple model (Kao et al., 2000), extending such a  $Q_0$  model to generate regional and sub-national predictions of propensity for transmission of *H. contortus*.

Results of the present study suggest that the  $Q_0$  model shows promise as a spatial predictor of the climatic risk of ovine haemonchosis, notwithstanding its simplifying assumptions. Hence, the model was able to explain a substantial portion of the variation in the dominance of *H. contortus* in grazing sheep across different geo-climatic zones. Following the conclusions of Heesterbeek and Roberts (1994), Roberts (1995) and

Kao et al. (2000), this promises that  $Q_0$  can be used as part of risk assessments to determine the extent to which parasite control strategies should take specific account of *H. contortus* in specific regions in current and projected future climates.

The  $Q_0$  model was adapted to a GIS in combination with gridded climatic datasets to consider how finer scale (sub-national) variations in climate could be harnessed to predict local risks of *H. contortus* transmission. Comparison of  $Q_0$  and  $Q_{0t}$  suggests temperature rather than moisture limitation to be the main driver of the seasonal and regional variations in the observed haemonchosis risk across the UK. However, rainfall appeared to exert some limitation on the transmission potential of *H. contortus* in mid-summer in some years, especially in the south of the UK. This was predicted to become more common in future under current climate change scenarios. A similar pattern was predicted for blowfly strike caused by *Lucilia sericata*, by Rose et al. (2011). However, sporadic summer rainfall limitation on parasite transmission was projected to be compensated by a longer simulated transmission season in future, and increased risk especially in the North. This resonates with recent observations of spread of *H. contortus* in Scotland (Kenyon et al., 2009) and the general trend for increasing records of clinical haemonchosis across the UK (Van Dijk et al., 2008). This is also in tune with existing knowledge of the life cycle of this species, which among gastrointestinal nematodes has a relatively high thermal requirement for development (O'Connor et al., 2007; 2008; Kahn, 2010; Morgan and Van Dijk, 2012).

A limitation of the  $Q_0$  approach is that dynamic changes in farm management are not considered, even though these are likely to be important factors in parasite epidemiology (Morgan and Wall, 2009) and on-farm management (Rahmann and Seip, 2006; Morgan and Van Dijk, 2012). For example, climatic risk might not translate into infection pressure if animals are housed and not grazing at the time. More sophisticated models are likely to be needed for a holistic understanding of parasite infection risk and suitable adaptation responses (Rose et al., 2015). Nevertheless, the simple models presented here could be useful to address strategic questions of the changing epidemiology of parasites in sheep, and to equip farmers with information on risk that could drive effective, targeted treatment (Kenyon et al., 2009; Charlier et al., 2014b). In this sense, transposing parasite prediction models onto GIS platforms offers hope for better links between climate-driven predictions of disease risk and control actions on the ground (Chanda et al., 2012).

While such platforms are increasingly within technical reach due to improvements in computer power and the availability of high-resolution climate data, parasitological data are rarely available, especially without bias (Musella et al., 2014). Moreover, bespoke studies at this scale to validate predictive spatio-temporal models of parasite risk are likely to be prohibitively expensive in most cases, and inherently limited when considering future climate change scenarios. Point validation of key predictions might be more feasible, using models to identify testable hypotheses. However, efficient and meaningful methods of testing model predictions are needed before they can be accepted more widely by stakeholders as useful tools in support of sustainable parasite control.

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Complementary supplement material: detailed definition and parameter estimates for the  $Q_0$  model

## The lifecycle model

The  $Q_0$  model was based on the life cycle of *Haemonchus contortus* (Fig. 1). Four key biological processes drive the dynamics observed through time in the lifecycle model. They are: egg production by adult parasites, development of infective larvae ( $L3$ ), chance of ingestion of  $L3$ , and establishment in the host following ingestion of  $L3$ . Arrows entering the box represent biological processes that lead to increases in the population of the stage in question, while the arrow leaving the box represent biological process that decrease stage-specific population. State variable abbreviations are given in Fig. 1.

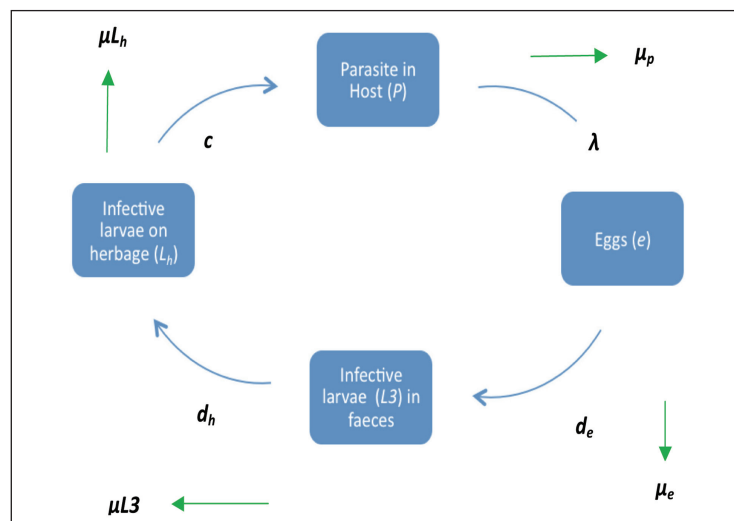


Fig. 1. Flow diagram illustrating the lifecycle model of *H. contortus*.  $p$  = parasite in host;  $L3$  = infective larvae in faeces;  $c$  = ingestion rate of herbage;  $\lambda$  = fecundity;  $d$  = development and migration rate;  $L_h$  = infective larvae on herbage;  $e$  = egg;  $\mu$  = mortality rate for each stage.

Adult parasite burden in host ( $P$ )

The adults within the host lay their eggs and die at a constant rate, as we assumed we are dealing with naïve host population. The rate of change in the adult population in the host(s) is therefore described by:

$$P_t = P_{t-1} (1 - \mu_p) + L_{h(t-1)} c p_e \quad (\text{eq. 1})$$

where  $\mu_p$  is the mortality rate of adult worms in the host;  $\lambda$  the fecundity (eggs per female parasite per day);  $c$  the ingestion rate of herbage (kg per day);  $p_e$  the proportion of  $L3$  establishing;  $t$  the present time; and  $(t-1)$  the previous time step (one day).

Eggs ( $E$ )

The rate of change in the egg population through the time on pasture (per hectare) is described by:

$$E_t = E_{t-1} (1 - \mu_e - d_e) + P_{t-1} \lambda_b / 2A \quad (\text{eq. 2})$$

where  $P$  signifies adult parasites;  $h$  host number;  $A$  the area grazed (hectare);  $\lambda$ : fecundity (eggs per female worm per day);  $d_e$  the development rate of the deposited eggs;  $\mu_e$  the mortality rate of the deposited eggs;  $t$  present time; and  $(t-1)$  the previous time step (one day).

### Infective larvae in faeces ( $L_3$ )

The rate of change in the population of  $L_3$  in faeces (per hectare) is described by:

$$L3_t = L3_{t-1} (1 - \mu_{L3} - d_b) + E_{t-1} d_e \quad (\text{eq. 3})$$

where  $d_e$  signifies the development rate of the deposited eggs;  $\mu_{L3}$ : the mortality rate of  $L_3$  in faeces;  $d_b$  the migration rate of  $L_3$  out of faeces onto herbage;  $t$  present time; and  $(t-1)$  the previous time step (one day).

### Infective larvae on herbage ( $L_b$ )

The rate of change in population of  $L_3$  on pasture (per kg herbage biomass) is described by:

$$Lh_t = Lh_{t-1} (1 - \mu_{Lb} - c_b / A) + L3_{t-1} d_b / b \quad (\text{eq. 4})$$

where  $d_b$  signifies the migration rate of  $L_3$  out of faeces onto herbage;  $L_b$  infective larvae on herbage (number per hectare);  $\mu_{Lb}$  the mortality rate of  $L_b$ ;  $c$  the ingestion rate of herbage (kg per host per day);  $b$  herbage biomass (kg per hectare);  $t$  present time;  $(t-1)$  the previous time step (one day).

### Parameter estimation

Field and laboratory studies that provided data on the effects of change in climate on the above parameters were surveyed. Linear or exponential or polynomial regression, as appropriate, was used to determine the slope, intercept, significance of relationship as well as the 95% confidence intervals (CI). The choice of regression for parameterization of any of the variable parameters was determined by which of the three regressions gave a good fit with the greatest statistical significance.

### Parameter values

#### Mean fecundity rate - the daily egg production rate per female worm ( $\lambda$ )

The mean fecundity rate is the daily egg production rate per female worm. Since we are dealing with naïve hosts, studies that provided data on daily mean peak egg production per female worm were included in the estimation of  $\lambda$  (Table 1).  $\lambda = 6,431$ .

Table 1. Values of mean daily fecundity ( $\lambda$ ) of *H. contortus* in naïve host.

| Source                   | $\lambda$ | Range        |
|--------------------------|-----------|--------------|
| Coyne et al., 1991a      | 6,582     |              |
| Coyne et al., 1991b      | 7,037     | $\pm 1337$   |
| Gordon, 1958             | 7,500     | 5,000-10,000 |
| Dineen and Wagland, 1966 | 6,334     | 5163-7504    |
| Coyne and Smith, 1992    | 4,700     | $\pm 632$    |
| Average                  | 6,431     | $\pm 1211$   |

#### Adult worm mortality rate - the daily instantaneous rate per parasite per day ( $\mu_p$ )

Since we assumed that we are working with a naïve host population, the best estimate for  $\mu_p$  for the present model was determined from single infection studies with parasites counted at short intervals. Thus data presented in experimental results of Barger and Le Jambre (1988) and Coyne et al. (1991b) were included in parame-

terization of  $\mu_p$  (Table 2). Altogether, nine replicates were sourced; they were averaged to arrive at 0.04 as the mean instantaneous mortality rate per worm per day ( $\mu_p$ ) with 95% confidence interval of  $\pm 0.037$  (Table 2).

Table 2. Values of daily mortality rate of adult worm sourced from relevant studies.

| Source                     | Replicate | Mortality rate | Range         |
|----------------------------|-----------|----------------|---------------|
| Barger and Le Jambre, 1988 | 1         | 0.01           | $\pm 0.002$   |
|                            | 2         | 0.036          | $\pm 0.005$   |
| Coyne et al., 1991a        | 1         | 0.0266         | $\pm 0.0206$  |
|                            | 2         | 0.0210         | $\pm 0.0170$  |
|                            | 3         | 0.0383         | $\pm 0.0140$  |
|                            | 4         | 0.0423         | $\pm 0.0074$  |
|                            | 5         | 0.0696         | $\pm 0.0167$  |
|                            | 6         | 0.0678         | $\pm 0.0121$  |
|                            | 7         | 0.0447         | $\pm 0.0068$  |
| Average                    |           | 0.04           | $\pm 0.03673$ |

#### *Development rates - the instantaneous daily development rate ( $d_e$ )*

In order to estimate  $d_e$ , studies providing data on the effect of temperature on successful development of 50% of the egg population to  $L3$  in faecal pellets, were used. Hsu and Levine (1977) reported time to 50% development of eggs to  $L3$  as a proportion of the maximum number of  $L3$  recovered. Rose (1963), on the other hand, reported minimum and maximum development times of egg to  $L3$ . From the data, we estimated  $d_e$  by as the mean development time from both minimum and maximum times. However, analysis of data from the former study indicates that the estimated mean times from Rose (1963) do not represent exactly the 50% development of the eggs to  $L3$ . Nevertheless, inclusion of data from Rose (1963) gave a more sensible model; hence its inclusion in estimating  $d_e$  (Table 3). For the present model,  $d_e$  for each data point =  $-\ln(\pi)$ ; where  $\pi$  = proportion developed  $^{(1/\text{time})}$ .

Table 3. Parameter values for estimating daily instantaneous development rates; sourced from Rose (1963), Hsu and Levine (1977).

| Temperature (Celsius) | Daily instantaneous development rate, $d_e$ | Source               |
|-----------------------|---|----------------------|
| 25.5                  | 0.25  | Rose, 1963           |
| 20.5                  | 0.0667                                      | Rose, 1963           |
| 15.5                  | 0.0476                                      | Rose, 1963           |
| 10.5                  | 0.0333                                      | Rose, 1963           |
| 20.5                  | 0.12  | Hsu and Levine, 1977 |
| 25.5                  | 0.225                                       | Hsu and Levine, 1977 |
| 30.5                  | 0.235                                       | Hsu and Levine, 1977 |
| 35.0                  | 0.25  | Hsu and Levine, 1977 |

Instantaneous development rates were used as estimated in Rose et al. (2015).



Table 3.1. Development rate of eggs - the instantaneous rate per parasite per day ( $d_e$ ).

| Source                | Slope | Intercept | Linear Function          | P-value | Confidence interval (CI) |
|-----------------------|-------|-----------|--------------------------|---------|--------------------------|
| Rose (1963)           | 0.011 | -0.097    | $y = 0.011T - 0.097$     | <0.01   | Slope: $\pm 0.00161$     |
| Hsu and Levine (1977) |       |           | $T = \text{temperature}$ |         | Intercept: $\pm 0.0385$  |

*Migration rate of L3 - instantaneous daily migration rate ( $d_b$ )*

For the present  $Q_0$ , changes in daily environmental conditions at the microclimate level of the herbage are considered crucial determinant of  $d_b$ . Data from Van Dijk and Morgan, (2011) were used for parameterization.

Table 4. Parameter values for estimating daily migration rates; sourced from Rose et al., 2015.

| Temperature (Celsius) | Daily instantaneous migration rate (Number) |
|-----------------------|---|
| 8                     | 0.2458                                      |
| 10                    | 0.2226                                      |
| 15                    | 0.3352                                      |
| 20                    | 0.2547                                      |
| 25                    | 0.1784                                      |
| 33                    | 0.1745                                      |

*Daily mortality rate of eggs - the instantaneous daily mortality rate of eggs ( $\mu_e$ )*

Data from the studies of Todd (1976a) was used to estimate  $\mu_e$  for the present model. The study specifically provided the lethal effects of temperature at the lowest and highest extremes that preclude egg development, thereby focusing only on mortality rates. In effect, this leaves a big gap between the two thermal extremes; however, this is not important for the present model, because within this temperature range, eggs would presumably develop before mortality becomes a limiting factor, provided that adequate moisture is available. Proportions of eggs surviving in faeces over time at each temperature were analysed based on the method used by Azam et al. (2012).  $\mu_e$  for each data point was then estimated using the formula:  $-\ln(\pi)$ ; where  $\pi$  is the proportion that died at each temperature point. All instantaneous rates at each temperature point were combined for the final regression (Table 5).

Table 5. Parameter values for estimating daily instantaneous mortality rates of eggs; sourced from Todd (1976a).

| Temperature (Celsius) | Daily instantaneous mortality rates of eggs (number) |
|-----------------------|--|
| 4                     | 0.089  |
| 4.5                   | 0.378  |
| 45                    | 1  |

Importantly, only exponential regression of all instantaneous rates sourced from Todd (1976a) gave a good fit as well as a statistical significance ( $P < 0.05$ ), hence the choice of the exponential regression for this parameter. It was also possible to reproduce  $\mu_e$  based on the outcome of Todd (1976a). ANOVA ( $F(1, 1) = 0.652$ ,  $P < 0.05$ ).  $R^2 = 0.583$  (see Table 5.1).

Table 5.1. Mortality rate of egg - instantaneous rate per parasite per day ( $\mu_e$ )

| Source               | Slope | Intercept | Exponential Function   | P-value | Confidence interval (CI)                      |
|----------------------|-------|-----------|------------------------|---------|---|
| Todd et al., (1976a) | 0.042 | 0.1514    | $y = 0.1514e^{0.042T}$ | <0.05   | Slope: $\pm 0.3655$<br>Intercept: $\pm 0.139$ |

### *Mortality rate of infective larva in faeces - instantaneous daily mortality rate of L3 ( $\mu_{L3}$ )*

Review of the available literature revealed studies by Todd (1976a,b) as the only relevant studies for estimating  $\mu_{L3}$  for the  $Q_0$  model. The two studies provided thermal effects from lowest to highest temperature extremes. Proportions of  $L3$  surviving in faeces over time at each temperature were estimated based on the methods described in Azam et al. (2012), and  $\mu_{L3}$  for each data point was estimated using the formula:  $-\ln(\pi)$ , where  $\pi$  is the proportion of  $L3$  that died at each temperature point. All instantaneous rates at each temperature point were combined for the final regression (Table 6).

Table 6. Parameter values for estimating daily instantaneous mortality rates of infective larvae in faeces; sourced from Todd (1976a,b).

| Temperature (Celsius) | Daily instantaneous migration rate of eggs (number) |
|-----------------------|---|
| 5                     | 0   |
| 20                    | 0.16  |
| 20                    | 0.175   |
| 25                    | 0.06  |
| 30                    | 0.165   |
| 30                    | 0.18  |
| 45                    | 1   |

Exponential regression of all rates sourced from Todd (1976a,b) gave a good fit with the most statistical significance and was able to reproduce  $\mu_{L3}$  based on Todd (1976a,b). ANOVA ( $F(1, 5) = 9.295$ ;  $P < 0.01$ ).  $R^2 = 0.806$  (see table 6.1).

Table 6.1. Mortality rate of L3 - instantaneous rate per parasite per day ( $\mu_{L3}$ )

| Source                 | Slope  | Intercept | Exponential Function   | P-value | Confidence bonus                              |
|------------------------|--------|-----------|------------------------|---------|---|
| Todd et al., (1976a,b) | 0.1082 | 0.005     | $y = 0.005e^{0.1082T}$ | <0.01   | Slope: $\pm 0.0227$<br>Intercept: $\pm 0.059$ |

### *Mortality rate of L3 on pasture - instantaneous daily mortality rate of L3/pasture ( $\mu_{Lb}$ )*

Mortality rate of  $L3$  on pasture is the only parameter in the third term of  $Q_0$  that is climate-driven; thus, the criteria for its estimation was based on including the effects of temperature ( $\mu_{L_{ht}}$ ) and rainfall ( $\mu_{L_{br}}$ ).

The temperature parameter estimation on mortality of  $L3$  on pasture ( $\mu_{L_{ht}}$ ) was based on the outcome of studies by Grenfell (1985), who found that the maximum-likelihood estimates of larval mortality rates in faeces and on herbage had the ratio of 3:1. Thus the already estimated  $L_3$  was divided by 3 to arrive at  $L_{ht}$  for the present model.

Effect of rainfall on mortality of  $L3$  on pasture ( $\mu L_{br}$ ) accounts also for moisture effects as considered by Banks (1990) and Onyali (1990). Both regard the mortality of  $L3$  as a function of either dry or wet climate, when temperature is non-limiting. Their conclusion was that rainfall as a source of moisture or wetness exerts significant effect on mortality of  $L3$  on pasture.

We used a daily geometric survival probability formula (Kao et al., 2000) for daily survival probabilities for dry and wet microclimates on pasture as estimated from Banks (1990) and Onyali (1990). This was done using the t-distribution as explained earlier (Tables 7). The assumption was that if daily survival probability is close to 1, the mortality rate of  $L3$  on pasture can be determined by subtracting survival probability from 1 (Kao et al., 2000). That is, daily  $L_{br}$ , whether dry or wet microclimate =  $1 -$  the daily survival probability. The estimated  $L_{br}$  was kept constant for each microclimate type, i.e. dry or wet.

Lack of rainfall in a week ( $P_{week} < 1\text{mm}$ ) was considered as dry microclimate at the level of  $L3$  on pasture (Banks et al., 1990; Onyali et al., 1990; Rose et al., 2015) or wet otherwise ( $P_{week} > 1\text{ mm}$ ).

Table 7. Daily survival probabilities for dry ( $S_d$ ) and wet ( $S_w$ ) microclimate at the level of  $L3$  on pasture, as estimated by Kao et al., (2000).

| Source              | $S_d$             | $S_w$               |
|---------------------|-------------------|---------------------|
| Banks et al., 1990  | 0                 | 0.873               |
| Banks et al., 1990  | 0.737             | 0.937               |
| Onyali et al., 1990 | 0                 | 0.892               |
| Average             | $0.246 \pm 1.243$ | $0.9006 \pm 0.0959$ |

Thus the daily  $\mu L_{bt}$  for dry microclimate =  $1 - 0.246 = 0.754$ , while it =  $1 - 0.9006 = 0.099$  for wet microclimate.

Therefore, the daily mortality of  $L3$  on pasture ( $\mu_{lh}$ ) for dry microclimate = daily  $\mu L_{bt}$  + daily  $\mu L_{br} = (L_3/3) + (0.754)$  and for wet microclimate = daily  $\mu L_{bt}$  + daily  $\mu L_{br} = (L_3/3) + (0.099)$ .

#### Standing biomass ( $b$ )

The standing biomass is a strong determinant of herbage intake rate per animal; therefore it provides basis to appreciate seasonality of  $L3$  transmission to grazing sheep. For the present  $Q_0$ , standing biomass was estimated as the mean of all data sourced and was set constant (Table 9).

Table 9. Values of standing biomass,  $b$  (kg of herbage per hectare).

| Source                   | $b$              | Comment  |
|--------------------------|------------------|--|
| Nicol and Thompson, 1982 | 2000             | Dried herbage was used in the spring season of New Zealand                 |
| Leathwick et al., 1992   | 1400             | Dried herbage was also used from early summer to mid-winter in New Zealand |
| Average                  | 1700 (1400-2000) |  |

#### Host density (stocking or host density per hectare ( $H$ ))

We assumed that host density on pasture will remain constant in all climatic and environmental conditions, hence the estimated value for host density was set constant; it was estimated to be 17 (Table 10).

Table 10. Values of host density per hectare of pasture from relevant studies.

| Source                    | <i>H</i>  | Comment  |
|---------------------------|-----------|--|
| Suarez and Buseti, 1995   | 14        | Ewes and lambs in extensive farm system during study |
| White and McConchie, 1976 | 8.65      | Merino wethers in semi-intensive farm system         |
| Brown et al., 1985        | 11.75     | Lambs in semi-intensive farm system                  |
| Barlow, 1985              | 11.25     | Ewes and lambs in extensive farm system during study |
| Miller et al., 1998       | 8.33      | Ewes and lambs in semi-intensive farm system         |
| Waller et al., 1981       | 30<br>35  | Ewes and lambs in extensive farm system during study |
| Average                   | 17 (8-35) |  |

*Herbage ingestion rate - herbage intake per weight in kg per host per day (c)*

The *L3* population was assumed to be evenly spread over pasture. The herbage ingestion rate was estimated using the formula: daily herbage intake per sheep divided by the available herbage or standing biomass (Kao et al., 2000), and was set constant. Daily herbage or standing biomass = 1,700 (estimated from Nicol and Thompson, 1982; Leathwick et al., 1992) (see Table 9). Daily herbage intake was calculated as 2.975 from the estimates of Paton (1984) and Leathwick et al. (1992) (Table 11). Both rates were also set constant; hence,  $c = 2.975 / 1,700 \approx 2.0 \times 10^{-3}$  ( $2.13 \times 10^{-3} - 2.38 \times 10^{-3}$ ).

Table 11. Values of herbage intake per weight in Kg per host per day (Leathwick et al., 1992; Paton et al., 1984).

| Source                 | Herbage intake (kg/day) | Comments |
|------------------------|-------------------------|----------|
| Leathwick et al., 1992 | 1.45                    | Lamb     |
|                        | 0.725                   | Lamb     |
| Paton et al., 1984     | 0.8                     | Lamb     |
| Total                  | 2.975                   |          |

*Probability of larval establishment - daily establishment rate of ingested L3 per ingested infective larvae ( $p_e$ )*

Since we are working with naïve host populations, data for estimating  $p_e$  were sourced from single-infection experiments; however, very few published estimates are available. Barger and Le Jambre, (1988) and Coadwell and Ward, (1981) provide the only ones based on single infections; estimations from these studies were averaged to arrive at a constant  $p_e$  (Table 12).

Table 12. Estimates of probabilities of *L3* establishment within host ( $P_e$ ); from results of single-infection experiments in non-immune sheep.

| Source  | Herbage intake/Kg/day | Comments   |
|---|-----------------------|--|
| Barger and Le Jambre, 1988                        | 0.59                  | $\times/\div 1.2$ ; single infections of group of sheep with doses of <i>L3</i> (4,000-16,000) |
| Coadwell and Ward, 1981 (Barger and Jambre, 1988) | 0.83                  | Lambs, single infection with 25,000 <i>L3</i> .  |
| Average   | 0.71                  | Margin of uncertainty: $\pm 0.05$  |

*Introduction of rainfall effects into the  $Q_0$  model*

Although there is lack of data on rainfall or moisture requirements for the survival and development success of the free-living stages of *H. contortus* we were able to include a workable rainfall function into the model. This was done by the heuristic deduction of rainfall rules from the relevant literature (Onyali et al., 1990; Banks et al., 1990; O'Connor et al., 2006; Wang, unpublished data). These rules provided the threshold of moisture requirement for the survival, development and migration success or failure of the free-living stages, given the time and overlapping cohorts. Essentially, the rainfall rules determine the effects of moist or drought conditions on the availability and transmission potential of the *L3* to grazing host.

*Separation of the effects of rainfall from those of temperature in the  $Q_0$  model*

Additionally, we were able to utilize the sourced data on the effects of temperature on the availability of *L3* for sheep infection, to estimate all the temperature-driven parameters (Rose, 1963; Todd 1976a,b; Hsu and Levine, 1977; Barger and Le Jambre, 1988; Coyne 1991b; Wang, unpublished data). Thus, making it possible to run the model based only on temperature effects -  $Q_{0t}$ . This also gives the basic reproduction quotient model the capability to identify when and where moisture would limit or preclude transmissions of *L3* to the host. Moreover, the objective of a climate-based  $Q_0$  necessitates the inclusion of rainfall effects in the model (Heesterbeek and Roberts, 1994; Robert, 1995; Kao et al., 2000). To this end, the estimation of temperature-based parameters and derivation of the rainfall rule made it possible to separate the effects of temperature from those of moisture on the free-living stages of *H. contortus*. Sources of validation data for the cross-regional comparison of  $Q_0$  with observed haemonchosis are given in Table 13, which provide the data arranged chronologically according to the Koeppen-Geiger climate classification.



Table 13. Details of data sourced for the validation and reliability test of the  $Q_0$  model across different geo-climatic locations.

| Location<br>(city country)   | Koeppen-Geiger<br>climate classification*              | Methods for estimating<br>haemonchosis level           | Time period    | Sources                     |
|------------------------------|--|--|----------------|-----------------------------|
| Ghana                        | Tropical rainforest (Af) and<br>Tropical savannah (Aw) | <i>Post mortem</i> recovery of<br>adult worms          | 1994-95        | Agyei, 1997                 |
| Cuba                         | Tropical savannah (Aw)                                 | <i>L3</i> recovery from pasture                        | 2000-01        | Garcia et al., 2006         |
| Mozambique                   | Tropical savannah (Aw)                                 | Identification of <i>L3</i> by<br>cultured faecal eggs | 1978-79        | Specht, 1982                |
| Nigeria                      | Tropical savannah (Aw)                                 | <i>Post mortem</i> recovery of<br>adult worms          | 1987-88        | Fakae, 1990                 |
| The Gambia                   | Tropical savannah (Aw)                                 | <i>Post mortem</i> recovery of<br>adult worms          | 1990-91        | Fritsche et al., 1993       |
| Ethiopia                     | Tropical rainy (Aw) and<br>Hot semi-arid (Bsh)         | <i>Post mortem</i> recovery of<br>adult worms          | 2004           | Sissay et al., 2007         |
| Haryana, India               | Steppe climates (Bs)                                   | <i>Post mortem</i> recovery of<br>adult worms          | 1977           | Gupta et al., 1987          |
| Lahore, Pakistan             | Steppe climates (Bs)                                   | <i>Post mortem</i> recovery of<br>adult worms          | 2006-07        | Qamar et al., 2009          |
| Western Pampas,<br>Argentina | Steppe climates (Bs)                                   | <i>Post mortem</i> recovery of<br>adult worms          | 1986-87        | Suarez and Buseti, 1995     |
| Senegal                      | Dry desert (Bwh) and<br>Steppe climate (Bs)            | <i>Post mortem</i> recovery of<br>adult worms          | 1982-83        | Vercruysse, 1985            |
| Hyderabad,<br>Pakistan       | Dry desert (Bw)  | Identification of <i>L3</i> by<br>cultured faecal eggs | 2004-05        | Al-Shaibani et al., 2008    |
| Punjab                       | Hot desert climate (Bw)                                | Identification of <i>L3</i> by<br>cultured faecal eggs | Year not given | Jabeen et al., 2000         |
| Faisalabad,<br>Pakistan      | Hot dry desert (Bwh)                                   | <i>L3</i> recovery from pasture                        | 2000-01        | Iqbal et al., 2005          |
| Saudi Arabia                 | Dry desert (Bwh)                                       | <i>Post mortem</i> recovery of<br>adult worms          | 1991-92        | El-Azazy, 1995              |
| Islamabad,<br>Pakistan       | Humid subtropical<br>(Cwa; Cfa)                        | Identification of <i>L3</i> by<br>cultured faecal eggs | 2005           | Chaudary et al., 2007       |
| Zimbabwe                     | Temperate highland tropical<br>(Cwb; Cwc)              | <i>L3</i> recovery from pasture (on<br>pasture)        | 1994           | Pandey et al., 1994         |
| Brazil                       | Maritime temperate<br>(Cfb; Cfc; Cwa)                  | <i>Post mortem</i> recovery of<br>adult worms          | 1981           | Charles, 1989               |
| United Kingdom               | Temperate<br>(Cfb; Cfc; Cwb; Cwc)                      | Identification of <i>L3</i> by<br>cultured faecal eggs | 2004-05        | VIDA, Met Office            |
| Netherland                   | Marine west coast (Cfb)                                | <i>L3</i> recovery from pasture<br>(on pasture)        | 2001           | Eysker et al., 2005         |
| Greece                       | Mediterranean (Csa)                                    | <i>L3</i> recovery from pasture<br>(on pasture)        | 1997-98        | Theodoropoulos et al., 1998 |
| Naples, Italy                | Mediterranean (Csa)                                    | <i>Post mortem</i> recovery of<br>adult worms          | 2005-06        | Rinaldi et al., 2009        |
| Turkey                       | Mediterranean (Csa)                                    | <i>Post mortem</i> recovery of<br>adult worms          | Year not given | Tinar et al., 2005          |
| Albany, Australia            | Mediterranean climate (Csb)                            | <i>L3</i> recovery from pasture<br>(on pasture)        | 1985           | Besier and Dunsmore, 1993   |
| Quebec, Canada               | Humid continental<br>mild summer (Dfb)                 | <i>L3</i> recovery from pasture<br>(on pasture)        | 2007           | Mederos et al., 2010        |
| Ontario, Canada              | Subarctic (Dfc; Dfb)                                   | <i>L3</i> recovery from pasture<br>(on pasture)        | 2007           | Mederos et al., 2010        |

\*Aw = tropical savannah; Bw = hot desert; Bs = hot semi-arid; Cw = subtropical; Cf = oceanic; Cs = Mediterranean; Df = continental.